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The Patch Distributed Producer-Scrounger Game

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Abstract

Grouping in animals is ubiquitous. However grouping is thought to provide individuals with foraging and antipredatory advantages, parasitic strategy often emerges in a group. If parasitic strategy cannot simultaneously search for food itself and parasitize other foragers, the success of parasitic strategy within any group is likely to be dependent on its frequency. The optimal parasitic policy has given rise to the producer-scrounger (PS) game model, in which producers search for food patches, and scroungers parasitize the discovered patches. The N-persons PS game model constructed by Vickery et al. (Vickery, W. L., Gireldeau, L., Templeton, J. J., Kramer, D. L., and Chapman, C. A., 1991. Producers, scroungers, and group foraging. American Naturalist 137, pp. 847-863) predicts the evolutionarily stable strategy (ESS) of frequency of producers ($\hat{q}$) that depends on the advantage of producers and the number of foragers in a group. However, the model assumes that the number of discovered patches in one time unit never exceeds one. In reality, multiple patches could be found in one time unit. In the present study, we relax this assumption and assumed that the number of discovered patches depends on the producers' variable encounter rate with patches (λ). We show that $\hat{q}$ strongly depends on λ within a feasible range, although it still depends on the advantage of producer and the number of foragers in a group. The basic idea of PS game is the same as the information sharing (parasitism), because scroungers is also thought to parasitize informations of locates of food patches. Horn referred the role of information parasitism in animal aggregation as early as 1968 (Horn, H. S. 1968. The adaptive significance of colonial nesting in the brewer's blackbird (*euphagus cyanocephalus*). Ecology 49, pp. 682-646). Our modified PS game model shows the same prediction as the Horn's graphical animal aggregation model. Hence, if we consider food patch distribution and

multiple patches could be found in one time, the PS game model is able to explain animal aggregation. In this study, therefore, we compare our λ-dependent PS game model not only to Vickery's original PS game model but also to Horn's graphical animal aggregation model.

Keywords : information-parasitism, group foraging, animal aggregation, Evolutionarily Stable Strategy, Horn's model

Introduction

Group foraging is widely assumed to be advantageous for animals. Two of its major benefits are lower predation hazard and increased foraging efficiency (Clark and Mangel 1986) (e.g., increased foraging rate (Clark and Mangel 1984; Vickery et al. 1991), reduced risk of starvation (Caraco 1981), and increased ability to capture elusive prey (Ward and Enders 1985)). For example, Horn (1968) proposed a graphical model of the spatial distribution of Brewer's blackbird (*Euphagus cyanocephalus*) nests in light of foraging efficiency. The model assumes territorial and colonial nesting, and in order to minimize the average distance from nest to food, territorial nesting would be expected when the distribution pattern of the food is uniform. When the distribution pattern of the food is temporally and spatially clumped, colonial nesting would be favored. For colonial nesting, Horn (1968) suggested that there is an additional advantage: information sharing (information-parasitism) between individuals in the same colony, which makes it possible for a bird who is foraging with little success to follow a more successful bird to a better foraging area. The same argument was made in Clark and Mangel (1984). They conclude that when food is abundant, information as to location is not very valuable; if food is scarce but evenly distributed, little information is derived from searching. Hence, flocking is most valuable when food is both scarce and patchy (Clark and Mangel 1984). These social foraging interactions among individuals are common in group foraging of birds, and most common is the exploitation of others' efforts to find food (Brockmann and Barnard 1979).

Parasitism is important for group foraging because it produces both advantageous (e.g. lower predation hazard and increased foraging efficiency for parasitic strategy (Clark and Mangel 1986)) and disadvantageous effects (e.g. decreasing of food gains for

patch discoverer and/or depletion of food; tragedy of commons (Hardin 1968; Rankin et al. 2007)). In other words, if foragers have the option of using a parasitic strategy, they can choose group foraging with parasitism or solitary foraging without parasitism depending on the situation. The optimal parasitic policy has been analyzed by two theoretical models: the information-sharing (IS) model (Caraco 1981; Clark and Mangel 1984) and the producer-scrounger (PS) game model (Barnard and Sibly 1981; Vickery et al. 1991; Caraco and Giraldeau 1991; Giraldeau and Caraco 2000).

Traditionally, the IS model assumes that in a group of N foragers all individuals search for food independently while, at the same time, monitoring the behavior of other group members, thereby allowing unsuccessful foragers to exploit food clumps discovered by others (Caraco 1981; Clark and Mangel 1984; Beauchamp and Giraldeau 1996). In the IS models, therefore, if an individual can use parasitism, they always choose parasitic behavior.

The PS game model (Barnard and Sibly 1981) is an N-person alternative-option game in which individuals use the producer strategy to find food clumps and the scrounger strategy to partake in food clumps discovered by the producers. For the PS game to apply to a group foraging situation, two assumptions must be met. First, individuals can play either producer or scrounger, but cannot simultaneously play both producer and scrounger strategy. Second, the payoffs received by a scrounger must be highly negatively-frequency-dependent on the frequency of scroungers in the group (Barnard and Sibly 1981; Vickery et al. 1991; Caraco and Giraldeau 1991; Beauchamp and Giraldeau 1996; Giraldeau and Beauchamp 1999; Giraldeau and Caraco 2000). In the PS game model, even if individuals can use scrounging, they do not always choose scrounging behavior. When those two assumptions are met, the PS game model predicts

the mixed evolutionarily stable strategy (ESS) of producers and scroungers.

An analytical PS game model constructed by Vickery et al. (1991) predicts the ESS frequency of producers as a functions of the fraction of a producer's advantage to the total food items in a patch and the number of foragers in a group. However the model assumes the producer's encounter rate with food patches, the maximum number of discovered patches in one time unit is always one, and the ESS frequency of producers does not depend on the producer's encounter rate with food patches. In their model, it is assumed that the producer's encounter rate with food patches is nearly equal to zero; therefore, the number of discovered patches in one time unit never exceeds one. In reality, the producer's encounter rate with food patches depends on the environment of the foraging site, and multiple patches could be discovered in one time unit. In this study, therefore, we modify this assumption to the variable encounter rate, and investigate the occurrence of parasitism. If the producer's encounter rate with food patches increases, the number of patches discovered during one time unit is sure to multiply, and foragers might cease parasitism at a high encounter rate because the benefits of group foraging are reduced in such situations. Actually, some empirical studies manipulated the producer's encounter rate with food patches by altering the spatial distribution of food patches, and showed that this changes the proportional use of producers and scroungers (Giraldeau et al. 1990; Giraldeau and Livoreil 1998; Coolen et al. 2001; Coolen 2002).

We compare our modified PS game model to Vickery's original model (Vickery et al. 1991). In addition to this, we discuss the relationship between our modified PS game model and Horn's graphical model (Horn 1968), because Horn's model includes the original PS game model situation as an extreme colonial strategy. A colony is a one

of the animal aggregations, and some studies explained the evolutionary advantages of colonial breeding by information sharing (Ward and Zahavi 1973), and Barta and Giraldeau (2001) reappraise this hypotheses using the PS game model.

The PS game model

In Vickery's PS game model (Vickery et al. 1991), N individuals forage in sufficient proximity that group members playing scrounger can all detect and exploit the food uncovered by any of the group's producers. A food clump contains F items. The producer obtains a finder's advantage, a portion (a) of the patch ($0 \leq a < F$) that it can use exclusively before the scroungers arrive. The proportion of individuals playing producer is q, and the proportion playing scrounger is $1 - q$. The producer's encounter rate with food patches is λ. Once a producer finds a clump, $(1-q)N$ scroungers arrive in unison and divide the remaining food items ($A = F - a$) equally among the individuals ($n = 1 + (1 - q)N$). The currency of fitness is energy intake, I. Patch discovery occurs sequentially, and patch exploitation time is negligible, which means that there is no handling time. Each producer's expected intake (I_P) after T time units of foraging is

$$I_P = \lambda T(a + \frac{A}{n}). \tag{1}$$

The rate of encounter with scrounging opportunities is a function only of the number of producers (qN). The scrounger's expected intake (I_S) is

$$I_S = \lambda T q N \frac{A}{n}. \tag{2}$$

The ESS frequency of producers ($\hat{q}$) can be found by setting I_P equal to I_S and solving for q:

$$\hat{q} = \frac{a}{F} + \frac{1}{N} \tag{3}$$

The ESS frequency of producers ($\hat{q}$) depends on the fraction of a finder's advantage (a) to the total food items in a patch (F) and the foraging group size (N).

The λ-dependent PS game model

Vickery et al. (1991) supposed that patches are scarce so that the maximum number of discovered patches in one time unit is only one, and all scroungers in a foraging group rush to the discovered patch and exploit food items. This assumption is considered reasonable if the number of producers in a foraging group (qN) is a minority and if a producer's encounter rate with food patches (λ) is small enough. However, if qN is large and/or λ is not small, the number of discovered patches in one time unit might exceed one, and a number of those discovered patches might disperse scroungers in multiple exploiting groups. In such a scenario, the number of discovered patches in one time unit depends on qN and λ. We modified the PS game model, which assumes that the number of discovered patches in one time unit depends on the number of producers in the foraging group (qN) and the producer's encounter rate with food patches (λ). We call this modified PS game the λ-dependent PS game model.

All parameters in the λ-dependent PS game model are the same as in the original PS game model (Vickery et al. 1991). We assume that the number of discovered patches in one time unit is determined by binomial distribution, and scroungers are divided equally between all food patches discovered in one time unit. Assuming that when one producer finds a food patch, other i ($0 \leq i \leq qN-1$) producers find food patches during the same time unit, the producer's expected intake (I_P) after T time units is

$$I_P = \lambda T \sum_{i=0}^{qN-1} \binom{qN-1}{i} \lambda^i (1-\lambda)^{qN-1-i} \left(a + \frac{F-a}{1+\frac{(1-q)N}{1+i}} \right). \tag{4}$$

When j $(1 \leq j \leq qN)$ producers find food patches during one time unit, the scrounger's expected intake (I_S) after T time units is

$$I_S = T \sum_{j=1}^{qN} \begin{pmatrix} qN \\ j \end{pmatrix} \lambda^j (1-\lambda)^{qN-j} \left(\frac{F-a}{1+\frac{(1-q)N}{j}} \right). \tag{5}$$

Because $i = j - 1$, I_P can be written by j as

$$I_P = T \sum_{j=1}^{qN} \begin{pmatrix} qN-1 \\ j-1 \end{pmatrix} \lambda^j (1-\lambda)^{qN-j} \left(\frac{F-a}{1+\frac{(1-q)N}{j}} \right) + T \sum_{j=1}^{qN} \begin{pmatrix} qN-1 \\ j-1 \end{pmatrix} \lambda^j (1-\lambda)^{qN-j} a. \tag{6}$$

As the first term in this expression is $I_S \times j/qN$ $(j \leq qN)$, there is a possibility that a producer's expected intake equals a scrounger's expected intake $(I_P = I_S)$. The ESS frequency of producer $(\hat{q})$ is solved by equaling eq. 5 with eq. 6, which can be simplified as follows:

$$\sum_{j=1}^{qN} \begin{pmatrix} qN-1 \\ j-1 \end{pmatrix} \lambda^j (1-\lambda)^{qN-j} \left(\frac{F(j-qN)+aN}{j+(1-q)N} \right) = 0 \tag{7}$$

This equation cannot be solved analytically, so we solve it numerically to find the ESS frequency of producers $(\hat{q})$.

In the numerical analysis, fixed values are the number of members in a foraging group (N), the number of food items in a patch (F), and the producers' encounter rate with food patches (λ). Variable values are the finder's advantage (a) and the proportion of producers (q). For example, we fix $N = 2$, $F = 10$, and $\lambda = 0.1$. Then, we change a from 0 to F and q from $1/N$ to 1, and find the combination of a and $\hat{q}$, which satisfies $I_P = I_S$ (eq. 7). In this example, there are two combinations of a and $\hat{q}$: $a = 0$ $(a/F = 0)$, $\hat{q} = 0.5$ $(1/2)$ and $a = 5$ $(a/F = 0.5)$, $\hat{q} = 1$ $(2/2)$.

Figure 1 shows the ESS frequency of producers ($\hat{q}$) represented by stepwise lines in a/F-q dimension with the number of foragers in a group (N) as 10. The stepwise solid line describes the original PS game model ($\hat{q} = a/F + 1/N$). The stepwise dotted lines describe the λ-dependent PS game model, for which the producers' encounter rate with food patches (λ) is fixed at 0.01, 0.1, 0.3, 0.5, 0.7, and 0.9. $\hat{q}$ increased as λ increased, and λ of the original PS game model is nearly equal to zero ($\lambda \simeq 0$). Therefore, even though $\lambda = 0.01$, the $\hat{q}$ of the λ-dependent model is sometimes higher than that of the original PS game model (Fig. 1).

Figure 2 shows the borderlines between group foraging with parasitism (coexistence of producers and scroungers) and solitary foraging without parasitism (producers only) in $\lambda - a/F$ dimension. When λ is small, the coexistence of producers and scroungers has a wide range for a/F, and this range is wider with a larger N. However, it becomes narrower as λ increases and the difference between N diminishes at a large λ.

Figure 3 shows the four examples of the number of foragers in a group (N) (2, 4, 8, and 16) of the original PS game model, and one combined (superimposed) graph of these four examples. In the original PS game model, the slope of the ESS frequency of producers ($\hat{q}$) is unity in a/F-q dimension ($\hat{q} = a/F + 1/N$), so that the $\hat{q}$ of a larger N never exceeds that of a smaller N (superimposed graph). In the λ-dependent PS game model, however, the $\hat{q}$ of a larger N sometimes exceeds that of a smaller N (Fig. 4; $\lambda = 0.3$).

Discussion

We modified the PS game model proposed by Vickery et al. (1991) to the λ-dependent PS game model, which assumes that the number of discovered patches in one time unit

depends on the producer's encounter rate with patches (λ). The ESS frequency of producers ($\hat{q}$) depends on three parameters for the λ-dependent PS game model (λ, a/F, and N), and we will discuss these parameters' effects on the polymorphic $\hat{q}$ (coexistence of producers and scroungers) comparing with Vickery's original PS game model. First, we will discuss the length of one time unit in the PS game model because λ relates to it. Second, we will discuss the effect of the variable λ on $\hat{q}$, and the relationship between the λ-dependent PS game model and Horn's graphical nesting model (Horn 1968). Third, we will discuss the effect of finder's advantage (a/F) on $\hat{q}$. And finally, we will discuss the effect of the number of foragers in a group (N) on $\hat{q}$.

The length of one time unit in the PS game model

λ describes a producer's encounter rate with food patches, so that if a producer searches for food patches for T time units, the number of patches discovered by each producer is λT. When we set $\lambda = 0.01$, it means that a producer finds one food patch in 100 time units. Then, how long is one time unit in the PS game model? In the original PS game model (Vickery et al. 1991), patch exploitation time is assumed to be negligible because patches are scarce in foraging areas, so search time is long relative to exploitation time. Ignoring exploitation time means that one time unit includes the events following foraging: a producer finds a food patch and consumes the finder's advantage (a) before scroungers arrive, and the producer and scroungers ($1 + (1 - q)N$) consume the remaining food items ($F - a$). In the PS game model, all these events occur in one time unit, and this is the length of one time unit implied in the PS game model. In the original PS game model, λ is set to make food finding an extremely rare event. If food finding events are not rare, how a situation of PS game will change? We discuss this effect connecting with animal aggregation in the following section. .

The effect of a variable λ on $\hat{q}$ and the relationship between the λ-dependent PS game model and Horn's model

In the λ-dependent PS game model, the ESS frequency of producers ($\hat{q}$) at a given producer's advantage (a/F) increases as λ increases (Fig. 1). $\hat{q}$ of λ-dependent PS game model is the same or larger than that of original PS game model (Vickery et al. 1991) in all range of $\lambda > 0$. If λ increases, the number of discovered patches in one time unit increases and scroungers are equally divided between each patch so that producers and scroungers gain an equal amount of food even if a/F is not large. In addition to this, the ratio of coexistence of producers and scroungers become smaller in the a/F dimension and all foragers end up producers as λ increases, meaning that foragers cease group foraging with parasitism (Fig. 2). The PS game condition is assumed to occur when not every forager is equally successful at foraging, so that some foragers parasitize other foragers' information of food. Therefore, if λ is large enough and each forager is successful, they do not need to parasitize for information and the PS game (parasitism) situation would dissolve. Some empirical studies showed the same trend with this prediction when the spatial distribution of food patches are distributed more (Giraldeau et al. 1990; Giraldeau and Livoreil 1998; Coolen et al. 2001; Coolen 2002).

When the food distribution is considered and multiple patches can be found in one time unit, the PS game model is able to connect with a subject of animal aggregation; group foraging (grouping) or solitary foraging (solitariness). This is the same situation in Horn's graphical model of whether colonial or territorial nesting is favored (Horn 1968). When λ is large, it is the same as when the distribution pattern of food is uniform, and territorial nesting (solitary foraging) would be expected. On the other hand, when λ is small, it is the same as when the distribution pattern of food is

temporally and spatially clumped, and colonial nesting (group foraging) would be favored. Hence, the λ-dependent PS game model shows the same predict of Horn's graphical nesting model (Horn 1968). Barta and Giraldeau (2001) also use the PS game to reappraise information-based hypotheses that explains the evolutionary advantages of colonial breeding.

The effect of a/F on $\hat{q}$

As well as the original PS game model (Vickery et al. 1991), a/F plays an important role in the coexistence of producers and scroungers, but the effect of a/F on $\hat{q}$ in the λ-dependent PS game model is smaller than that of the original PS game model. When λ is less than 0.5, producers and scroungers are able to coexist unless a/F is less than 0.5 and the number of foragers (N) is less than 4 (Fig. 2). When λ increases, however, even though a/F (advantage of producers) is small enough, the strategy of producer is favored and the PS game (group foraging with parasitism) condition could not occur at any N. In the original PS game model (Vickery et al. 1991), on the contrary, producers and scroungers are always able to coexist at any N if a/F is less than 0.5.

The positive effect of N on $\hat{q}$ in the λ-dependent PS game model

In the original PS game model (Vickery et al. 1991), $\hat{q}$ at a given a/F decreases as N increases. This is obvious from the $\hat{q}$ equation: $\hat{q} = a/F + 1/N$. And, even if we fix $\hat{q}N$ as an integer, $\hat{q}$ of a larger N never exceeds that of a smaller N (Fig. 3). Because the maximum number of discovered food patches in one time unit is only one, the number of scroungers gather in the patch ($(1-q)N$) increases as N increases, so that the increasing of N causes a only negative effect on producers. Conversely, in the λ-dependent PS game model, the number of discovered food patches in one time unit

increases as λ and N increase, and scroungers are equally divided between those food patches, so that the difference of $\hat{q}$ between various N at a given a/F becomes smaller as λ increases. When we fix $\hat{q}N$ as an integer, available $\hat{q}$ increases and the increment decreases little by little as N increases, and $\hat{q}$ of the bigger N exceeds that of the smaller N at some given a/F (Fig. 4). This positive effect of N on $\hat{q}$ is never seen in the original PS game model (Vickery et al. 1991). In the λ-dependent PS game model, if the food patches are abundant in the foraging area, the food intake per individual does not decrease as N increases. Therefore, the aggregation of foraging individuals keeps up and N becomes larger. As we mentioned above, however, the PS game condition often occurs around small λ, so this case might be rare.

Additional Considerations

As we described above, the effect of λ on $\hat{q}$ is not negligible in the PS game. Therefore, when we apply the PS game model, we have to check the λ of the intended species and foraging area. In this study, we assumed that each patch has a finite renewable resource for simplicity, so that a binomial distribution is used to calculate the predicted number of discovered food patches in one time unit. In reality, however, patches are usually a finite resource that do not instantaneously replenish. Hence, a hypergeometric distribution might be more appropriate for the foraging situation of some species of birds, which are often used for test of PS game model. In addition to this, other probability distribution functions (negative binomial (hypergeometric) distribution, uniform distribution, etc.) should be used according to the distribution of food availability.

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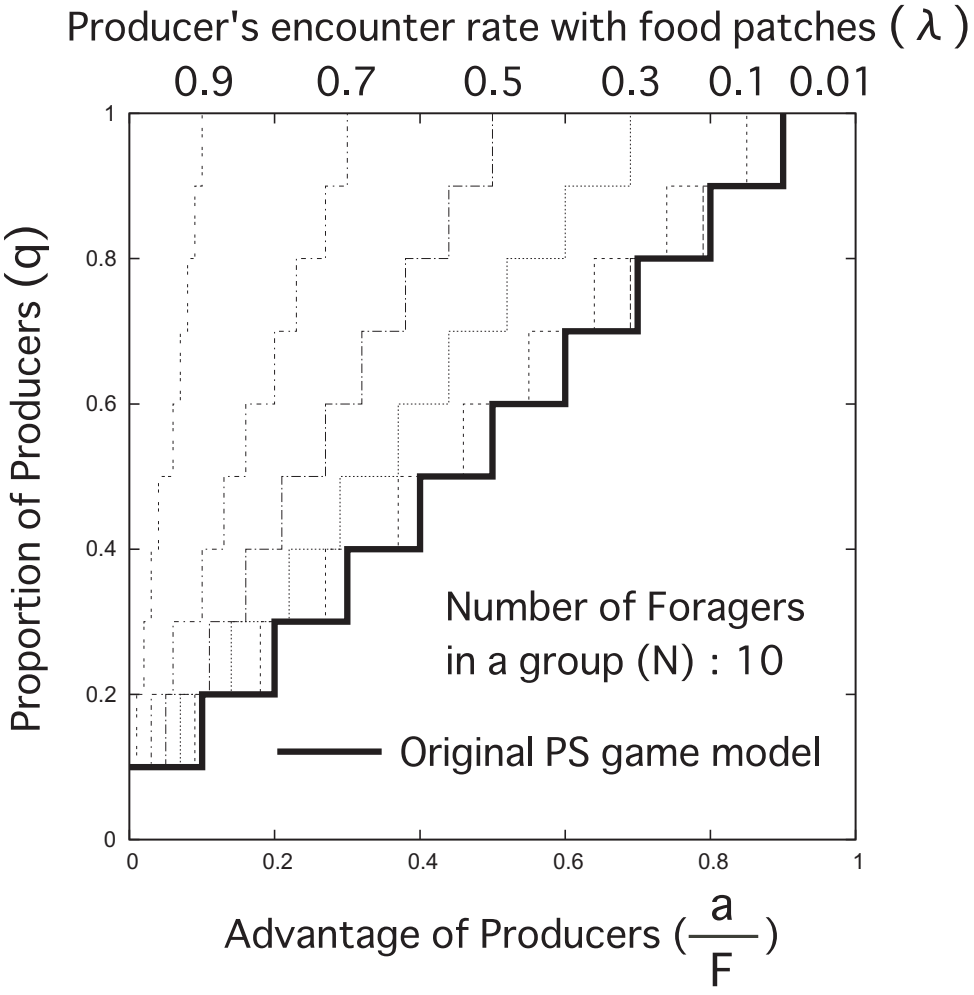
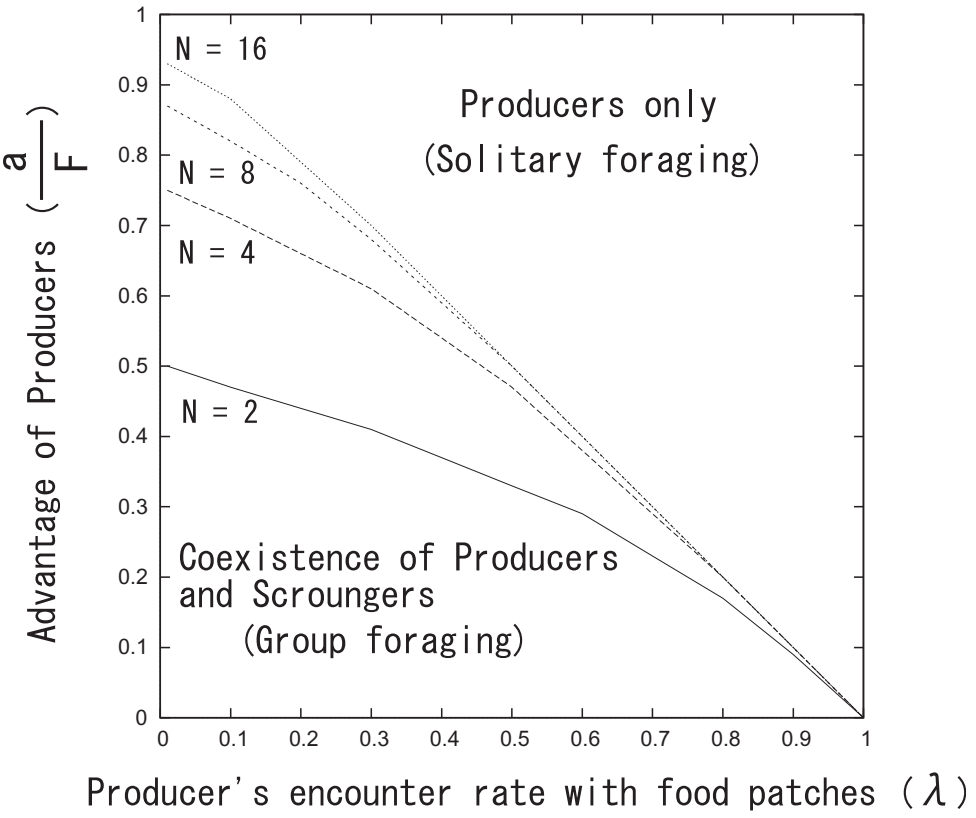
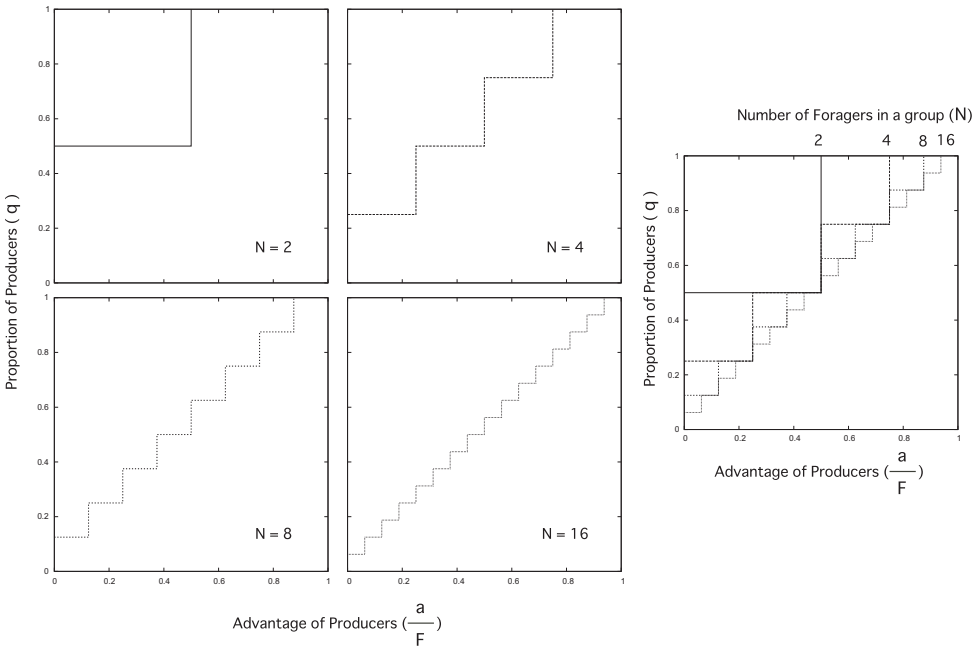

Producer's encounter rate with food patches (λ)
0.9
0.7
0.5
0.3
0.1
0.01
Proportion of Producers (q)
0
0.2
0.4
0.6
0.8
1
Number of Foragers
in a group (N) : 10
Original PS game model
Advantage of Producers (a/F)


N = 16
N = 8
N = 4
N = 2
Producers only
(Solitary foraging)
Coexistence of Producers
and Scroungers
(Group foraging)
Advantage of Producers (a/F)
Producer's encounter rate with food patches (λ)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1


Proportion of Producers (q)
N = 2
N = 4
N = 8
N = 16
Advantage of Producers (a/F)
Number of Foragers in a group (N)
2
4
8
16
Proportion of Producers (q)
Advantage of Producers (a/F)

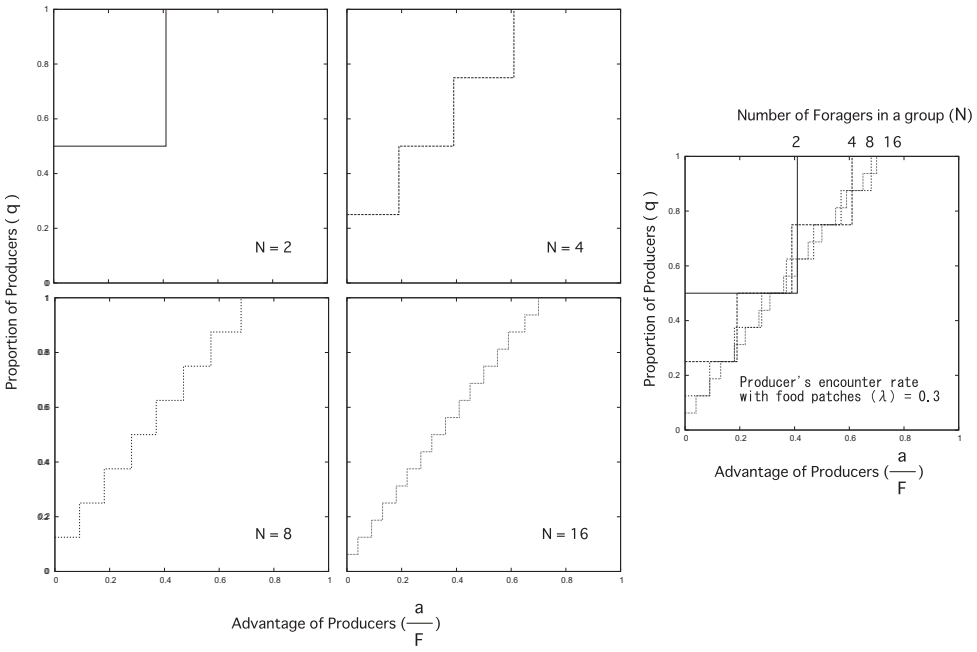

Proportion of Producers (q)
N = 2
N = 4
N = 8
N = 16
Advantage of Producers (a / F)
Number of Foragers in a group (N)
2 4 8 16
Producer's encounter rate
with food patches (λ) = 0.3
Advantage of Producers (a / F)

Figure 1: The ESS frequency of producers of $N = 10$

The solid line is the original PS game model and the others lines are $\lambda = 0.01$, 0.1, 0.3, 0.5, 0.7, 0.9.

Figure 2: Borderline between group foraging and solitary foraging

The line describes the maximum fraction of producer's advantage (a/F) at which producers and scroungers can co-exist.

Figure 3: The ESS frequency of producers in the original PS game model

The left-hand side of figure shows four examples of ESS frequency of producers $(\hat{q})$ in $N = 2$, 4, 8, and 16. The right-hand side of figure combines these four examples.

Figure 4: The ESS frequency of producers in the λ-dependent PS game model with $\lambda = 0.3$

The left-hand side of figure shows four examples of ESS frequency of producers $(\hat{q})$ in $N = 2$, 4, 8, and 16. The right-hand side of figure combines these four examples.